A STUDY OF DRYOPHANTA ERINACEI (MAYR) AND ITS GALL.*

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CONTENTS

INTRODUCTION.

The Cynipidae constitute, biologically, one of the most interesting families of the Hymenoptera. They have long attracted attention, not only from the systematic view-point, but also from the view-point of their life-history, the variety of the galls they produce or inhabit, their biology, and the cause of gall formation. The purpose of this paper is to present an intensive study of one gall-maker *Dryophanta erinacei* (Mayr), discussing its life-history, its parasites, its guests, and the cause of gall formation.

The Oak Hedgehog Gall is rounded or oblong, with the surface finely netted with fissures, and more or less densely covered with spines. It varies in length from 10-15mm., and occurs on both sides of the White Oak leaf. The point

*Contribution from the Entomological Laboratory of Cornell University.

of attachment is generally on the midrib (Fig. I, Pl. I), though it is often found on the lateral veins. When young it is yellowish green, but in autumn it becomes yellowish brown, much lighter in color than the tinting of the leaf. The gall first appears late in June, and reaches full development about the third week in August. It is widely distributed, having been reported from New England, North Carolina, Iowa, Illinois, Indiana, Kansas, Michigan, Ohio, Virginia, Canada, and probably Florida and Colorado.

A longitudinal section through the gall shows that it contains several chambers varying from two to eight in number. These I have named according to their location. First to be noted are the *central cavities*, (Fig. 2a, Pl. I), which measure 2mm. x 3mm. and are located in the central portion of the growth. These are occupied by Dryophanta erinacei and the parasites. Second, there are the *lateral cavities*, (Fig. 2b, Pl. I), situated at the side and base of the growth and measuring 1½mm. x 2mm. These are occupied by inquilines. Lastly, there are to be found the *peripheral cavities*, (Fig. 8a, Pl. II), located on the coriaceous portion of the gall, and covered with the basal layer of spines. These are 1mm. in size, and are likewise occupied by iniquilines.

The gall was first described by Walsh in 1864 under the name Cynips q. erinacei. When Mayr in 1881 established the genus Acraspis he included the insect causing this gall, which therefore was known as Acraspis erinacei. The first description of the insect appeared in a paper by Beutenmüller '09, entitled "Species of Biorhiza, Philonix, and their allied Genera, and their Galls," in which he places it in the genus Philonix. As will be shown later in this discussion, the insect belongs to the genus Dryophanta, and should be known therefore as Dryophanta erinacei (Mayr).

The Life-History of Dryophanta Erinacei.

The agamic form of Dryophanta erinacei emerges from the oak hedgehog gall about the fifth of November. It varies from 1.50 to 3mm. in length. The head is black, rufous on both sides of the face, finely punctate, with whitish pubescence; antennae black, fourteen jointed, with basal joints rufous; thorax rufous; plurae black with rufous mark anteriorly; all minutely punctate; parapsidal grooves distinct posteriorly,

obsolete anteriorly; scutellum rufous, punctate and pointed posteriorly; metathorax black; abdomen piceous; ventral spine and tip of abdomen hairy; legs yellowish rufous, tibia slightly darker; wings aborted.

The insect makes its way to the leaf and flower buds of the white oak, where oviposition takes place. On the tree where our observations were made, it continued to emerge and oviposit until the twenty-first of November. The insects are most active on cold days or early in the morning. During the warm weather they are inactive and sluggish, hiding at the base of the petioles, in the crotches of the young shoots, or in the crevices of the bark. They have been taken in this vicinity on rare occasions in early December, but usually they succumb to the first heavy frosts at the close of November.

Its method of oviposition does not differ much from that already described by Kieffer for other species of the Cynipidae which attack buds. The insect clasps the apical portion of the bud with the second pair of legs, (Fig. 3, Pl. I), and pressing alternately with the first and third pair produces a teetering motion which forces the ovipositor into the buds. The long ovipositor lifts the apical edge of the outer scale, and is gradually pressed down along the edge of succeeding scales, and finally thrust into the region of the young leaf and flower. Then there is a sudden jerk of the body which curves the distal end of the ovipositor, turning the openings against the concave face of the innermost scale. The insect now retains a motionless attitude for almost four minutes, during which the egg is deposited. The ovipositor is then withdrawn, the passage being filled with a waxy substance for the protection of the egg. This waxy secretion is doubtless from the accessory glands of the reproductive system, and is homologous with the secretions with which Corydalis cornuta, certain of the Lepidoptera, as the Apple Tent-Caterpillar, the Tussock-moths, and many other insects cover their eggs.

The egg, (Fig. 20, Pl. III), is an oval body 400μ. x 225μ. provided with a pedicel which is 1mm. in length. It is attached by this pedicel to the upper brown portion of the scale, falling either against the green portion of the scale (Fig. 6, Pl. II), or being held among the young leaves or flowers, in which position it remains during the winter. It is worthy of emphasis that this pedicel does not constitute the apical pole of the egg

since the larva emerges from the opposite pole, and as already indicated it serves as an appendage for attaching the egg to the bud scale.

As will be seen later the eggs of the Chalcids are flask-shaped, (Figs. 31, 32 and 37, Pl. IV), but here the elongate portion is in reality the cephalic portion of the egg. This is shown by the fact that the egg is oriented in the ovum in such a way that the elongate portion is cephalad. also that the larva always emerges at the base of the neck (Figs. 32 and 37, Pl. IV). This therefore, is exactly opposite to the condition found in Dryophanta erinacei.

Buds were examined on the eighth of May and the unhatched eggs found were very turgid, appearing slightly enlarged. On the twelfth of May a slight swelling, at the apex of which an empty egg shell was visible, appeared on the lower green portion of the scale, (Fig. 9, Pl. II). This proved to be a freshly formed gall, containing a young larva of Dryophanta erinacei. The gall at this stage was thin-walled, with a pebbled surface, greenish in color, and contained a watery fluid. The egg-shell remains attached to the apex of the gall until the latter has reached considerable size, when it dries up and disappears. These hypertrophies develop rapidly, as many as three appearing on one scale. The wall of the gall has by this time changed to a yellowish brown color, and soon becomes quite dry and brittle.

Galls also develop on the apical portion of the leaf and flower buds, (Fig. 10, Pl. II). These are red, being similar in color to the young leaf and flower. The wall is pebbled on the surface, and thin. The cavity contains a single larva bathed in a watery fluid, and similar in all respects to the one inhabiting the scale gall. The terminal galls are of the same size as those on the scales, varying in number from one to four, and when mature are reddish brown. Since only the agamic form of Dryophanta erinacei was found ovipositing on the leaf and flower buds, and since the eggs of this species and no other were found in the leaf and flower region, and since males and females similar in size and character emerge from the two galls, it is evident that they are produced by the same insect. The difference in color in the galls is due to the normal difference of the tissue of which they are formed.

Shoots were brought into the laboratory, placed in water and covered with bell jars. Here about noon on the twenty-first of May the first male and female emerged. They were quite vigorous, and about four-thirty in the afternoon the female was noticed actively moving along the midrib of the young leaf. Suddenly she stopped, and set up a rapid nodding motion which lasted thirty-five seconds, during which the ovipositor was thrust into the tissue. The insect remained motionless for a time, then withdrew the ovipositor, filling the passage with a yellow substance which, as in the agamic form, is probably a secretion poured forth by the accessory glands of the reproductive system. The process was repeated four times in succession without moving the body forward. Each time the ovipositor was inserted the body was curved slightly more than at the preceding puncture. The entire time occupied by the four ovipositions was from four-thirty-four to four-fifty, or sixteen minutes, thus allowing four minutes to each oviposition of which a little over two minutes and a half was occupied by the passage of the egg. Many other observations were made, and the time in all instances corresponded to the first recorded.

While the first observations of oviposition were made without having seen copulation occur, in all the following instances it was observed. The male strikes the female several times with the antennae, after which the latter rests quiet. The male then clasps her thorax latero-caudad of the second pair of wings with the second pair of legs, while the first pair rest on the dorso cephalic portion of the thorax, and the third pair extend slightly latero-cephalad of the abdomen; copulation takes place, lasting for a few minutes.

The egg of the sexual form, (Fig. 25, Pl. III), is oval, 160μ x 450μ. provided with a pedicel 750μ. in length, which is shorter than in the agamic form. It is always placed in the fibro-vascular bundles, and at an angle of about $80°$ to the axis of the leaf. The egg differs from that of the agamic form only in the elongate portion being shorter.

The larva is characteristic of the Cynipidae, having a slightly depressed head, fine needle-like mandibles, broad thorax, and reflexed pointed abdomen. During development the abdomen does not become as enlarged as in the agamic form. The thorax also continues prominent throughout all

larval stages, which is not the case with the agamic form. Fig. 27, Pl. III, represents a mature larva of the sexual form, and may be compared with Fig. 19, Pl. III, which represents a mature larva of the agamic form in the corresponding stage.

In the open the adults did not emerge until the twenty-ninth of May, and continued to oviposit from that time until the fifth of June. Oviposition here was as observed in the laboratory, the time occupied corresponding exactly to that already noted. Fig. 4, Pl. I, shows a female of the sexual form.

The sexual form which possesses the characteristics of the genus Dryophanta may be described as follows:

Female: Color. Head, thorax and abdomen shining black, nonpubescent; mandibles yellowish brown; mouthparts yellow; antennæ first two joints yellowish, flagellum shading to black at the tip. In the male the entire antennæ are black. Length 2mm.

Head: Face opaque, surface irregular, rugose about the ocelli; compound eyes 200μ.x300μ. Distance between compound eyes and hind ocelli 75μ.; between hind ocelli 100μ.; between compound eyes and fore ocelli 500μ. Distance between compound eyes and antennæ 75μ.; between antennæ 75μ. Width of head at temples 1.50mm.; mandibles tridentate, mouth parts as in Figs. 21, 22, and 23, Pl. III. Antennæ fourteen jointed,(Figs. 28 and 29, Pl. III).

Thorax: Smooth, parapsidal furrows distinct posteriorly, obsolete anteriorly, pluræ smooth.

Scutellum: Rugose, becoming smooth in front, cross furrow reduced to a shallow depression (Fig. 26, Pl. III).

Appendages: Wings hyaline, fringed with setæ, veins yellowish brown, (Fig, 24, Pl. III); legs yellowish, coxæ of the third pair yellowish brown.

Abdomen: Smooth, deeper than long, first segment one-third the size of the abdomen, outline of the remaining segments as seen from the side serrate; ventral spine and tip of abdomen hairy.

Male: Color. Same as female, length 1½mm.

Head:	Distance	of compound eyes to hind ocelli	50μ
	"	between hind ocelli	150μ
	"	of compound eyes to fore ocelli	600μ
	"	of compound eyes to antennæ	50μ
	"	between antennæ	50μ

Antennæ fifteen jointed.

Thorax: Mesonotum more gibbous than in female.

Abdomen: Petiolated, longer than deep as seen from the side; petiole cylindrical.

On the twenty-fifth of June the first evidences of gall-formation appeared on the leaf-veins, the hypertrophied tissue pushing through the slightly ruptured epidermis. The

embryoes obtained at this stage measured $125\mu.$–$130\mu.$. In galls gathered on the first and second of July, larva were found measuring 374μ. These were similar to the young larva which give rise to the sexual form, having a slightly depressed head, sharp pointed mandibles, broad, prominent thorax, and pointed, reflexed abdomen. During the summer, molts were observed after which the larva measured 500μ, 750μ., $1\frac{1}{4}$mm., $1\frac{3}{4}$mm., $2\frac{1}{4}$mm., respectively, thus showing five stages during the life-history. Fig. 19, Pl. III, shows a larva $1\frac{3}{4}$mm., obtained about the middle of August. From this time, the thorax does not show a great increase in size, but the abdomen loses its reflexed character, becomes globose, and increases in size until pupation. The first pupa was obtained on the fifth of September, but the adults did not emerge until the fifth of November. Fig. 5, Pl. I, shows a pupa of the agamic form.

Thus we have another illustration of dimorphism in the Cynipidae, the agamic form of Dryophanta erinacei developing in the oak hedgehog gall on the white oak leaves, emerging and ovipositing in the leaf and flower buds of the same tree, from which, in scale and terminal galls, the sexual form develop. These, emerging, oviposit on the veins of the white oak leaves, and their offspring cause the oak hedgehog gall.

The Parasitic and Inquiline Life in the Gall.

The oak hedgehog gall is not merely the abode of the maker, but also of several parasites and inquilines. In order to obtain a knowledge of these, their mode of life, their relationship to the maker, and to each other, we shall consider them under the following heads:

A. Parasitic and inquiline life as shown by breeding experiments.

B. Parasites in relation to Dryophanta erinacei and to each other during gall development.

C. Inquilines, their relation to Dryophanta erinacei, to the parasites, and to each other during gall development.

Parasitic and Inquiline Life as shown by Breeding Experiments.

The breeding experiments were of a twofold character. First, galls were placed in cages, and the species inhabiting them bred out. Second, larva were studied individually in order to obtain larval characters, and then bred out and thereby related to the adults.

I. Leaves bearing galls were gathered, separated from the grass and other leaves, then placed in cardboard boxes at one end of which a test-tube was inserted. In these tubes the insects gathered, and were easily collected. The galls were divided into two classes—those gathered when the leaves were falling from the tree, and those subjected to snow, frost, and general winter conditions for one and two months respectively. The leaves were moistened once a week in order to keep the galls from drying up, and thus preventing the adults from emerging. The parasites appeared first, but the inquilines did not emerge until the last of February.

The parasites, of which eight different species were obtained, belonged to the family Chalcididæ, and were all known to be parasites in the oak galls. The inquilines belonged to the Cynipidæ, genus Synergus. The following table will give the various species, and the number of each obtained.

TABLE I.

Decatoma flava (Ashmead)	600	specimens
" querci-lana-dorsalis (Fitch)	1	specimen
" varians (Walsh)	30	specimens
Eurytoma studiosa (Say)	75	"
" auriceps (Walsh)	30	"
Ormyrus ventricosus (Ashmead)	150	"
Syntomaspis sp.	15	"
Tetrastichus sp.	10	"
Synergus erinacei (Bass.)	70	"

II. The larvæ were removed from the galls, and studied, and the larval characters determined. These specimens were bred out in order to connect with the adult form. The method employed was to note and tabulate such characters as the form of the mandibles, the arrangement and size of the setæ, and the general larval form of a large number of specimens. Each individual was then placed separately in a four dram vial which was sealed and set in a dark place. Four species were bred through to the adult. Both from the study of the larva in the

cavities, and the result of the breeding experiments, it was evident that the parasites inhabited the central cavities, while the inquilines, though occasionally found in this region, were mostly confined to the lateral and peripheral cavities.

Owing to the small percentage of several of the parasites as shown in Table I, we were able to breed out only five species. The descriptions of the larval forms obtained are as follows:

Decatoma flava: The larval form of this Chalcid, (Fig. 34, Pl. IV), when mature measured $1\frac{1}{4}$mm. It possesses slender bidentate mandibles, (Fig. 33, Pl. IV). The setæ are short and spine-like, arising from distinct, prominent tubercles, and are located as in diagram, (Fig. 42, Pl. V), six on the head, ten on the prothorax, eight on the mesothorax, six on the metathorax, and four on each of the abdominal segments.

The egg, (Fig. 32, Pl. IV), is flask-shaped and measures $200\mu.\times50\mu.$, neck $560\mu.$, and pedicel $56\mu.$ It is pigmented, and becomes brownish black on maturing. The long neck lies cephalad in the ovary of the adult, and the larva emerges from the egg at the base of the neck, (Fig. 32, Pl. IV). Thus the neck is not comparable to the long pedicel of the eggs of the Cynipidæ. The short, crooked pedicel at the opposite pole represents in atrophied form that found in the Cynipidæ.

Eurytoma studiosa and Eurytoma auriceps: The larval forms of Eurytoma studiosa and Eurytoma auriceps are so similar that it is impossible to determine specific characters. The one shown in Fig. 43, Pl. V, always bred out to Eurytoma studiosa during the winter, but during the summer larvæ corresponding in all respects to the diagram bred out to both Eurytoma studiosa and Eurytoma auriceps. Hence the general characters given here may be considered generic rather than specific. Fig. 35, Pl. IV, gives a general view of this larva.

The mature larva measures $1\frac{1}{4}$mm., having bidentate mandibles similar to that shown in Fig. 33, Pl. IV. The setæ are long, slender, with distinct tubercles, and give the body a very hairy appearance. The general distribution of these, (Fig. 43, Pl. V), is twelve on the head, ten on the prothorax, ten on the mesothorax, ten on the metathorax, six on the first abdominal segment, four on each of the second, third, and fourth segments, and six on each of the remaining segments. The larva can be readily distinguished from the larva of Decotama flava by the length of the setæ, those of the latter being short, spine-like, and fewer in number.

The egg is flask-shaped measuring $240\mu.\times144\mu.$, neck $720\mu.$, and pedicel $64\mu.$ The neck lies cephalad in the ovary of the adult, and the embryo emerges from the egg just at the base, (Fig. 37, Pl. IV). The pedicel is short, curved, and aborted. The egg is pigmented and becomes black on maturity. It is quite similar in form to the egg of Decatoma flava, but is slightly larger, and deeper in color when mature.

The egg of Ormyrus ventricosus is flask-shaped measuring $200\mu.\times120\mu.$, (Fig. 31, Pl. IV). In this Chalcid egg the pedicel is absent.

Synergus erinacei: The larva of Synergus erinacei, (Fig. 38, Pl. IV) —summer brood—is fleshy, 1mm. in length, and possesses tridentate mandibles, the second tooth of which is pointed like an arrow-head. The setæ are very small, difficult to locate, and without distinct tubercles at the base. Their location, (Fig. 44, Pl. V), is fourteen on the head, fourteen on the prothorax, twelve on the mesothorax, six on the metathorax, four on each of the eight following abdominal segments, six on the ninth, and eight on the tenth segment.

The egg is white, the body being kidney-shaped, $240\mu.x80\mu.$, and is provided with a long neck $440\mu.$, Fig. 39, Pl. IV, shows one of these.

The larva of Synergus erinacei (spring brood) is dark, fleshy, $700\mu.$ long, (Fig. 40, Pl. IV). The mandibles are tridentate, the central tooth blunt. The setæ are minute, without distinct tubercles, and distributed as in Fig. 36, Pl. IV, eight on the head, sixteen on the prothorax, ten on each of the meso- and metathorax, eight on each of the first three abdominal segments, and six on each of the remaining segments.

The eggs, two of which are shown in Fig. 41, Pl. IV, are white. The body is kidney-shaped $125\mu.x56\mu.$, and provided with a neck $410\mu.$ in length.

Parasites, their relation to Dryophanta erinacei, and to one another during the development of the gall.

The Chalcids, Decatoma flava, Eurytoma studiosa, and Eurytoma auriceps were observed ovipositing from June tenth to the fourteenth. The method in all cases was similar, but the time occupied during oviposition, and the number of eggs deposited differed.

Decatoma flava selected a spot on the midrib where Dryophanta erinacei had oviposited, thrust the long ovipositor down alongside the same channel, and deposited an egg in contact with that of the Cynipid. The ovipositor was then withdrawn, and the opening sealed. This required three minutes.

Eurytoma studiosa and Eurytoma auriceps each selected a spot about the region where Dryophanta erinacei had oviposited, and forcing the ovipositor into the fibro-vascular bundles placed from one to six eggs near, but not in contact, with the egg of the Cynipid. The eggs are usually laid in clusters, and appear black in the tissue of the leaf. The opening is sealed on the withdrawal of the ovipositor. The time consumed by these two species in oviposition was four minutes each.

When the larva of Dryophanta erinacei emerges from the egg, it proceeds at once to form a cavity which encloses the eggs surrounding it. In newly-forming galls the cavity is small, and the egg of the parasites is frequently found resting in

the abdominal angle of the larva of Dryophanta erinacei. Here it often hatches. The larva breaks the shell near the base of the neck, (Fig. 37, Pl. IV.), and emerges, proceeding to attack the host in the abdominal region. If the Cynipid larva has just molted it is destroyed at once. If on the other hand, it escapes the attacks of the parasites during this period, they will live together until the next molt occurs, when the host is almost invariably killed and eaten. Only on rare occasions have the host and parasite been found living together in the same cavity until both have reached 1mm. in length.

If two parasitic larvæ of the same or different species are found in one cavity in the early stages, the stronger alone survives, for I never have observed more than one adult emerge from a single cavity. Since no Chalcid eggs are found in the cavities inhabited by the inquilines, we may conclude that the Chalcids are parasitic primarily on Dryophanta erinacei, and secondarily on one another.

The larva of Eurytoma studiosa and Eurytoma auriceps develop rapidly, and from the twenty-fourth of July to the first of August adults emerge, thus giving a summer brood. No adults of Decatoma flava emerge in the summer or autumn. After the parasites have destroyed the host, it is questionable whether they feed on the plant tissue, since the lining of the cavity they inhabit turns brown, becoming hard and brittle much earlier than is the case with the cavities occupied by Dryophanta erinacei.

It is impossible to determine absolutely the extent of parasitism in these galls, yet we gain some idea from the following. During four weeks 1050 galls were examined, which showed sixty per cent of parasitism not including the internal parasites which had not emerged from the maker.

Inquilines, their relation to Dryophanta erinacei, to the parasites, and to each other during the development of the gall.

The relation of the inquilines of this gall both to the host and to the parasites is very interesting, since they are present not only as guests, but also as parasites. The parasitic character of certain species of Synergus has already been pointed out by Möller and Mann, but nowhere have I found any record of their singular action as observed in this gall. Synergus erinacei is not only parasitic on Dryophanta erinacei, and the parasites

in the central cavities, but it carries its parasitic habits to the extent of mining from cavity to cavity, and having a meal out of the occupants.   Fig. 12, Pl. II shows where a larva of Synergus erinacei has mined from A-B, also one is already breaking down the wall at C.   Fig. XI, Pl. II shows where a larva of Synergus erinacei has mined from a lateral to a central cavity. In all, over eighty instances of mining have been observed.   On eighteen occasions we have fed Dryophanta erinacei and different Chalcid larva to the inquilines, but only once were we able to induce it to attack a larva of its own species.   The average time required by Synergus erinacei to consume a larva was 1½ hours.   Hence we see that the supposed guest is not only a plant feeder, but has shown itself to be a serious parasite among the occupants of the gall.

The Stimulus to Gall Production.

A. The Relation of the Malpighian Vessels to Gall Formation.

Investigators have generally agreed that galls cannot be produced apart from the presence of insects, but different theories have been presented as to the cause of the abnormal growth.   Adler (1881) points out that in Neuroterus lævius-clus and Biorhiza aptera, the gall is first caused by the insect wounding the surrounding cells with its fine mandibles, and that the growth of the gall is in some way dependent on the presence of the larva.   Cook (1903) in his publication ''Galls and Insects Producing Them,'' states that the Cynipidæ stimulate the plant to excessive growth by biting, and it is his contention that gall formation is primarily the result of mechanical stimulation.   Rössig (1904) in a paper entitled '' Von Welchen Organen geht der Reiz zur Bildungder Pflanzengalle aus?'' attributes a rôle to both oenocytes and the Malpighian vessels, and though regarding the latter as giving off an effective secretion, he attributes the primary source of this secretion to the oenocytes.

His studies of the Malpighian vessels are purely from the morphological standpoint, and are based on a limited and poorly selected variety of species.   He places great emphasis on the size of the cells constituting the vessels, and on the size of the vessels as compared with that of the larva.   Moreover he includes in his discussion species that do not produce galls by means of any product poured forth by the Malpighian

vessels, since the galls are produced before the eggs are hatched. Finally, he brings no evidence from a broad, comparative study of the Malpighian vessels of various gall-producing species to support his conclusion.

The condition found in the bud-gall from which the sexual form of Dryophanta erinacei emerges is as follows: The egg rests on the living portion of the scale. When the larva emerges a viscous mass is adhering to it, but outside of this is a clear fluid resembling the secretion of the Malpighian vessels both in color and in action on glass when exposed to the air. The young galls soon appear enclosing the larva. In this instance the secretion of the Malpighian vessels appears to provide the first stimulus to gall-formation. With the agamic form, where the egg is enclosed in the plant tissue, one cannot observe the process so easily.

On examining the galls of both the agamic and sexual forms of Dryophanta erinacei, it was noticed that the cavities were lined with growing tissue, abundantly supplied with chlorophyll, also that where the larva of Dryophanta erinacei rested, both it and the plant tissue were bathed at times with a colorless fluid. When the larva was placed on a glass slide it at once poured forth an abundance of this fluid, which always became opaque, milky white, on drying. By varying the position of the larva when placing it on a glass slide, this secretion was seen to pour forth from the anal region, while the head and thorax remained dry. About this time a study of sections of the larva revealed two tubules consisting of four cells each, which showed great activity. Longitudinal sections proved these to be cells of the Malpighian vessels, (Fig. 45, Pl. VI.).

The Malpighian vessels of the agamic form of Dryophanta erinacei consist of two long tubules containing fifty-six rounded cells, with large nuclei, and attached to the hind gut, just at its point of union with the mid-intestine, (Fig. 48, Pl. VI.). They are whitish in color, the cells varying in size according to the larval period. They reach their maximum in the fourth larval stage. These larval tubules do not give rise to the adult vessels, but, degenerating in the prepupal and pupal stages, give place to the adult tubules which arise as evaginations of the hind-intestine, just below the attachment of the larval vessels. They are the largest glands in the body, extending slightly ventrad along the mid-intestine, their cephalic ends

reaching beyond the point of union of the mid and fore-intestine in the region of the thorax, and are held in place by the fat tissue.   In a longitudinal section they appear as in Fig. 47 Pl. VI

The individual cells consist of a homogeneous cytoplasm in which vacuoles are found in the outer portion and also near the nucleus.   Secretions are sometimes seen in these.   The nucleus is irregular, and often greatly branched, sending long arms into the cytoplasm.   It is densely packed with chromatin granules.

The larva were mostly fixed in Dietrich's fluid, and stained with borax carmine and Lyons blue.   This proved very satisfactory for general work, but the best results were obtained when the larvæ were fixed in hot Gilson's fluid.

The cells are very active in secreting a colorless fluid during the period of gall-formation, which continues from the end of June until the middle of August.   At this latter time, the larva has reached the fourth stage, measuring $1\frac{3}{4}$mm.   There is somewhat of an increase in the size of the cells up to this point, which may be in proportion to the demand upon them.   After this there is a slight decrease to a constant size, which is retained until degeneration begins.   The following table shows the increase.

TABLE II.

	LENGTH	SIZE OF CELLS	
Larva	500μ	$64\mu.\text{x}72\mu.$	molt.
"	$750\mu.$	$64\mu.\text{x}80\mu.$	molt.
"	1mm.	$72\mu.\text{x}80\mu.$	
"	$1\frac{1}{4}$mm.	$72\mu.\text{x}82\mu.$	molt.
"	$1\frac{1}{2}$mm.	$72\mu.\text{x}88\mu.$	
"	$1\frac{3}{4}$mm.	$112\mu.\text{x}120\mu.$	molt.
"	2mm.	$72\mu.\text{x}96\mu.$	
"	$2\frac{1}{4}$mm.	$72\mu.\text{x}88\mu.$	molt.
"	$2\frac{1}{2}$mm.	$72\mu.\text{x}88\mu.$	

As pointed out earlier in this paper, molts occur at 500μ, 750μ, $1\frac{1}{4}$mm., $1\frac{3}{4}$mm., and $2\frac{1}{4}$mm.   It will be observed that the cells reach their maximum at the fourth stage, about which time the gall is rapidly maturing.   From this time, less and less secretion is poured out, and the linings of the cavities begin to lose their green appearance, gradually becoming yellowish brown, dry, and hard. Further, the larval form rapidly changes.   The abdomen increases in size, becoming globose, while the head and thorax show only small increase.   This is in striking contrast to the early stages.   A larva of the fifth stage, measuring $2\frac{1}{4}$mm., when placed on glass or any foreign substance excretes practically no fluid.

It was observed in all early stages that the excretion of the
fluid was under the control of the larva, being poured forth
freely when required. When a larva was found not feeding on
plant tissue the body was dry. When a parasitic larva rested
on the host both were bathed in a colorless fluid. If the larva
of Dryophanta erinacei was placed on a glass slide or foreign
substance, it immediately poured forth an abundance of fluid.
It was evident that a reserve must be retained in the tubules.
In a longitudinal section, (Fig. 45, Pl. VI.), it will be noticed
that the small proximal cells (indicated by *V*.) on each side of
the lumen are arranged so as to press closely against those
opposite. This formation appears constant throughout the
various stages, and we believe has a valvular function.

A number of tubules were dissected out from larva of the
earlier stages in normal salt-solution. This solution was
allowed to evaporate, and the salt crystals formed used in
grinding up the dried tubules. To the powdered mass a few
drops of normal saline were added, and when all was dissolved,
the fluid was filtered. The filtrate was treated with 85%
alcohol, and the action brought down a heavy, white, floculent
precipitate, which suggested that something of an enzymic
nature might be present. This phase of the investigation was
not pursued further at this time.

Fresh material was again obtained, the Malpighian tubules
dissected out as above, thoroughly dried, and ground with
powdered carborundum, which reduced them to a finer powder
than the salt-crystals. The powdered mass was dissolved in a
few drops of normal salt-solution and filtered. The filtrate
was injected with a hypodermic syringe into the midrib of the
white oak leaves, one drop being used to each puncture. The
operation was repeated three times on several leaves. Checks
were made, normal saline being used in these. The solution
containing the Malpighian tubule product penetrated from one-
fourth to one-half an inch in the fibro-vascular bundles of the
midrib. The tissue was turned yellowish brown, and cracking
appeared similar to that seen in many young leaves where the
gall formation has just started, but owing to the death of the
larva, has ceased. While these experiments did not produce a
gall, they give suggestions as to the work performed by the
secretion of the tubules. Nothing of the above described
appearance was to be seen in the checks.

From a further study of Table II, it will be seen that between the first and fourth larval stages there has been a considerable increase in the size of the cells which constitute the tubules. The greatest increase was between the third and fourth larval stages, which was coincident with the greatest growth of the gall, when it doubled in size. During this period the larva gives off the greatest amount of secretion from the Malpighian vessels. After this time, as already noted, the larval form changes, and the amount of secretion diminishes rapidly, so that a larva taken, say two weeks later, that is about the first of September, would not pour forth any secretion when placed on a foreign substance. The lining of the cavity is by this time quite dry, brittle, and deep yellowish brown in color.

Now, from the development of the Malpighian vessels, and the amount of secretion poured forth by them coincident with the gall development, also in view of the effect of this secretion when applied to the plant tissue in the experiments, it is evident that the Malpighian vessels have elaborated some product which when poured forth by the insect stimulates the surrounding plant tissue to rapid growth. In a few instances, we have found urate crystals in the lumen of the tubules, but urates are present in the Malpighian vessels of all insects, and, as Rössig has shown, chemically pure urates do not produce galls. Hence an additional factor is without doubt present in the secretion of the Malpighian tubules of Dryophanta erinacei, and this produces the effective stimulus.

The Malpighian Vessels of the Inquilines.

The Malpighian vessels of the inquilines were dissected out. They were white in color, and consisted of two slender tubules. These arise at the point of union of the mid and hind-intestine, having a broader attachment than that found in Dryophanta erinacei, (Fig. 60, Pl. VIII). The cells are smaller than those of D. erinacei, the nuclei more regular, and the lumen quite distinct. They show no evidence of great secreting activity, and in a longitudinal section appear as in Fig. 61, Pl. VIII. The larva when placed on a glass slide does not pour forth a secretion as does Dryophanta erinacei. Further, the species, though an inhabitant of a gall, does not emerge from the egg until the gall has attained considerable growth. Its eggs are

rarely found in the central cavities, but generally in the rapidly growing tissue of the gall, where, after emerging, it forms a cavity. Again the summer brood oviposit on the young galls in July, laying their eggs just beneath the soft outer layer. Here on hatching the larva forms a mere depression in the hard portion of the gall, the soft outer layer forming the other wall. It therefore gives rise to no gall formation. We have here, then, a species of the Cynipidæ, an inhabitant of a gall, appearing after the stimulus to abnormal growth has been given, and evidently not contributing to it. Its larval Malpighian tubules are less developed than those of Dryophanta erinacei.

The Malpighian Vessels of the Parasites Inhabiting the Gall.

The Malpighian vessels of a Eurytoma larva, as dissected out, are yellowish in color, larger than those of the inquiline, and four in number. There are two long, clavate tubules drawn to a point at their cephalic ends, and two short ones with blunt ends, (Fig. 62, Pl. VIII). These arise at the union of the mid and hind-intestine. The long tubules extend cephalad slightly ventrad of the mid-intestine beyond the point of union of the mid and fore-intestine in the thorax. The cells are smaller than those of Dryophanta erinacei, the nuclei more compact, and they do not give evidence of a high state of activity. Further, it must be remembered that the black eggs of these parasites are found only in the central cavities, and never in the tissue of the gall. Hence they are in a place where there is no demand for gall formation. Again, the galls are well developed, and the cavities of fair size before these emerge from the egg. Therefore they do not give rise to a chamber, as do both the maker and the inquilines. Moreover when placed on a glass slide or foreign substance they do not excrete a quantity of fluid, as do the larva of Dryophanta erinacei. Finally, when they have destroyed the host, the cavity lining loses its green, healthy appearance, passing from a yellowish brown to a deep brown color.

Now, considering the habits of the parasites—that they do not form a cavity, but occupy one already developed by Dryophanta erinacei, and feed upon this species—also that the cells of their Malpighian vessels do not give evidence of great activity, we must conclude that the size of the tubules provides no evidence that they produce a gall through their agency.

The larva of Decatoma flava also possesses four tubules. Two are long, clavate, and drawn to a point at their cephalic ends, and two are short with blunt ends, (Fig. 64, Pl. IX). They are more slender, the cells smaller, and the nuclei more regular than those of the Eurytoma larva. The general condition stated regarding the former also applies to Decatoma flava.

It is interesting to note that the galls that contain the highest percentage of parasites and inquilines, and those in which the larva of Dryophanta erinacei have been destroyed at an early stage never reach full development; also that the tissues become dry, hard, and brittle. It is largely from this type of gall that the summer brood of the inquilines, and of Eurytoma studiosa, and Eurytoma auriceps emerge.

The Malpighian Vessels of other Gall-Forming Cynipidæ.

In the agamic form of Holcaspis globulus (Fitch) the Malpighian vessels, as obtained from fresh material, are white in color. They consist of two long tubules with large, globose cells, and irregularly branched nuclei. They give evidence of a high state of activity, and on contact with a foreign substance pour forth a fluid as did Dryophanta erinacei. In the degeneration of the larval tubules and the development of those of the adult they are similar to Dryophanta erinacei, (Figs. 54, Pl. VII and 57, and 58, Pl. VIII).

The agamic form of Dryophanta polita (Bass.), which causes the polished oak gall, possesses two Malpighian vessels which as dissected out are white in color. They are smaller than those of Dryophanta erinacei and Holcaspis globulus. The cells are globose, nuclei irregular, and branched. Their general action is similar to those already discussed. In a longitudinal section they appear as in Figs. 55 and 56, Pl. VII. The process of degeneration of the larval tubules, and the development of the adult vessels correspond to that already described for Dryophanta erinacei. Fig. 55, Pl. VII, is a longitudinal section through a pupa of Dryophanta polita, which shows the degeneration of the larval tubules and the adult vessels forming.

The Malpighian Vessels of Gall-Producing Tenthredinidæ.

The larva of Nematus pomum (Walsh) which causes the willow-apple gall was secured. Longitudinal sections through the larva show cylindrical tubules arising at the union of the mid and hind-gut, and extending caudad, (Fig. 66, Pl. IX). A longitudinal section of the tubule is shown in Fig. 65, Pl. IX. The cells are numerous, small, and regular, the nuclei being symmetrical, and densely packed with chromatin. We have no evidence here of great activity, nor does the larva secrete any fluid when placed on a foreign substance.

Now it is known that the Tenthredinidæ do not produce galls in the same manner as the Cynipidæ, but the stimulus is given at the time of oviposition. Adler says ''I have carefully observed Nematus vallisnierii. The fly cuts into the tender leaves of the end shoot of Salix amygdalina, and inserts her eggs in the wound, frequently placing several in one leaf. At the same time some glandular secretion from the insect flows into the wounded leaf. A few hours after this injury, the leaf surface presents an altered appearance, and new cell-formation begins, freely leading to the thickening of the surrounding leaf surface. After the elapse of about fourteen days the green and red, bean-shaped gall is fully grown. If it is now opened the egg will be seen lying in the cavity. Three weeks elapse before the larva emerges from the egg.''

Thus it is evident that the Malpighian vessels of the Tenthredinid larva are not factors in gall production.

The Malpighian Vessels of the Gall-Producing Diptera.

The larva of *Trypeta solidaginis*, from the globular gall on the goldenrod, shows Malpighian vessels consisting of small, round cells containing spherical nuclei, (Fig. 68, Pl. IX). The cells show no evidence of exceptional activity, nor have we any reason to believe that the Malpighian tubules are here factors in gall formation.

The larva of *Cecidomyia strobiloides*, which causes the pine-cone willow gall, likewise shows Malpighian vessels of a normal type. The cells are small, very regular, and do not indicate any unusual state of activity, (Fig. 69, Pl. IX).

From a study of these two forms it seems probable that the galls which they form are not due to any product poured forth by the Malpighian vessels, for these neither secrete a fluid when in contact with a foreign substance, nor do the cells show any divergence from the normal type.

The Malpighian Vessels of Other Hymenoptera.

Since we have only considered species which form galls or are associated as parasites and inquilines with the gall-maker, it is necessary that we study related species that do not form galls, in order that this comparative study may be more complete.   For this purpose we have selected species of Braconids and Ichneumons.

A Braconid larva was obtained from the fall-webworm. A longitudinal section of this larva is shown in Fig. 67, Pl. IX. The cells of the Malpighian vessels are medium in size, and the nuclei irregular.   They are equal to those of the tubules of the Chalcids, and larger than those in the vessels of the inquilines.

The Ichneumon larva was secured from the red-humped apple-worm.   Sections through the Malpighian tubules showed that the cells were small and regular, the nuclei round.   Here we have a tubule the cells of which correspond in size to those found in the tubules of the inquilines.

The Degeneration of the Larval Malpighian Tubules.

The degeneration of the larval tubules, and the development of the adult vessels in the forms studied, are of such interest that, though in part discussed by Rössig, they may here be considered, and especially since the stages missed by Rössig can be supplied.

Degeneration of the larval Malpighian tubules commences in the prepupal stage.   The cytoplasm shows huge vacuoles, appears in shreds, and clings to the cell wall.   The nucleus becomes greatly elongate and branched, and chromatolysis sets in.   About this time small evaginations appear in the hind-intestine, which develop into cylindrical tubules.   Gradually the cells of the larval Malpighian vessels break down, and pass into the lumen of the hind-intestine, while the adult tubules with small cells, and regular nuclei elongate rapidly.

A series of the Malpighian vessels dissected out show this process (Figs. 48, 49, 52, and 53, Pls. VI, and VII).

The method of degeneration and the relation of the phagocytes to this process has been in question. In the process of degeneration as shown in Dryophanta erinacei, Holcaspis globulus, Dryophanta polita, and in the Eurytoma larva, it is clear that the phagocytes play no part whatever. The cells break down and pass into the alimentary tract. Fig. 50, Pl. VII is from a cross section of a larva of Dryophanta erinacei, and shows a fragment of a cell of a tubule found in the lumen of the intestine. Fig. 51, Pl. VII is from a longitudinal section of a similar larva, and shows the degenerating cell just breaking away into the lumen of the intestine. Figs. 54, and 57, Pls. VII, and VIII show the degenerating cells of Holocraspis globulus, also the adult vessels forming. Fig. 55, Pl. VII represents the same condition in Dryophanta polita.

The only instance where phagocytosis was found was in the larva of Trypeta solidaginis. Here as shown in Fig. 76, Pl. X, the phagocytes are present, but from a study of the slide it was evident that chromatolysis had already set in, and the phagocytes were only of secondary importance in the degeneration of the cell.

B. *The Relation of the Oenocytes to Gall Formation.*

We must now consider the relation of the oenocytes to the production of the gall. Rössig says "The oenocytes have a certain influence, in that they in some manner break up the blood fluid, and work it over in advance for the Malpighian vessels." This conclusion rests on the following: First, a mere comparison of the size of the oenocytes with that of the larva; second, "The general opinion that they are excretory organs destined to store up urates, especially, as Verson has shown in Bombyx, during the time when the Malpighian vessels do not carry out their function, during molting and pupation. Berlese is of the same opinion." Lastly, a possible correlation in the development between the Malpighian vessels and the oenocytes.

Rössig points out that the oenocytes of the various larva which he has studied reach an unusual size. This growth is attained within a short time, after which they shrink and

gradually degenerate.   Their size, in comparison with that of
the larva, is remarkable.   From some of the larva investigated
he gives the following:

	LENGTH	OENOCYTES	NUCLEI
Larva of Biohriza terminalis	470μ.	20μ.	
" " Andricus ostreus	375μ.	23μ.	
" " Andricus fecundatrix	450μ.	25μ.	
" " Dryophanta divisa (end of June)	460μ.	20–67μ.	25μ.
" " Dryophanta divisa (17th July)	600μ.	100μ	50μ
" " Dryophanta divisa (end of July)	785μ.	146–150μ.	59μ

From this, the author points out, first the unusual size of
the oenocytes as compared with that of the larva, and second
the three-fold increase in size of the oenocytes within one
month.   He also gives measurements of oenocytes found in the
inquiline inhabiting the gall formed by Andricus globuli, Vespa
crabro, Nematus vallisnierii, Hormomyis fagi, and Aphis mali.
With one exception, the larva are all larger than those of the
gall wasps, and their oenocytes smaller.   Now by a comparison
of the size of the oenocytes with that of the larva, and secondly
these oenocytes and larva with those of the gall-forming Cyni-
pidæ he endeavors to establish his theory.

In discussing the first point the author says "In no other
instance have such large oenocytes been found in so small a
larva."   Throughout his treatment of the oenocytes this fact
is kept continually in the foreground.   Mention is made of
Kochevnikov's discovery of a remarkable oenocyte 176μ. in a
pupa of a honey-bee 15mm.–16mm. in length, but the author
points out that, since the oenocytes in Dryophanta divisa are
so large as compared with the larva, and the latter so small
as compared with the pupa of the honey-bee, (that is, 785μ.
as compared with 16mm.), great importance must be attached
to the oenocytes of the gall wasps.

Now does the size of the cell in comparison with that of the
body determine its importance?   It is very doubtful if such
evidence can be used to support his conjecture regarding the
function of the oenocytes.

In the second place we must discuss the three-fold increase
of the oenocytes.   This appears to be tabulated from one set
of larva in a single species, but is not shown to be constant
throughout that species.   Now before a general conclusion can
be drawn, this triple increase would have to be shown to be
constant not only for a large number of larva of Dryophanta

divisa, but also in many species of the gall-forming Cynipidæ. In the following table it will be seen that in Dryophanta erinacei the oenocytes show no remarkable increase in size, and that they reach their maximum long after the Malpighian vessels have passed their period of greatest activity.

TABLE III.

D. ERINACEI.	LENGTH	OENOCYTES	NUCLEI
pupa		56μ.x64μ.	26μ.x32μ.
		64μ.x64μ.	32μ.x32μ.
		48μ.x48μ.	24μ.x24μ.
larva	2½mm.	80μ.x120μ.	32μ.x40μ.
		64μ.x 72μ.	32μ.x32μ.
		48μ.x 64μ.	32μ.x32μ.
"	2¼mm.	64μ.x 56μ.	32μ.x32μ.
		56μ.x 56μ.	24μ.x24μ.
		56μ.x 48μ.	24μ.x24μ.
"	2mm.	72μ.x 76μ.	32μ.x32μ.
		56μ.x 56μ.	24μ.x24μ.
		48μ.x 48μ.	24μ.x24μ.
"	1¾mm.	48μ.x 48μ.	32μ.x32μ.
		40μ.x 40μ.	24μ.x24μ.
"	1½mm.	56μ.x 56μ.	28μ.x28μ.
		48μ.x 48μ.	24μ.x24μ.
"	1¼mm.	48μ.x 52μ.	24μ.x24μ.
		48μ.x 48μ.	24μ.x24μ.
		40μ.x 40μ.	24μ.x24μ.
"	750μ.	40μ.x 48μ.	24μ.x24μ.
		40μ.x 40μ.	24μ.x24μ.
"	500μ.	40μ.x 40μ.	24μ.x24μ.
Eurytoma pupa		88μ.x 88μ.	40μ.x48μ.
		90μ.x 96μ.	48μ.x48μ.
		80μ.x 80μ.	40μ.x40μ.
Eurytoma larva	1¾mm.	88μ.x 80μ.	40μ.x36μ.
		64μ.x 64μ.	40μ.x40μ.
Synergus erinacei larva	1¾mm.	88μ.x 72μ.	32μ.x32μ.
		56μ.x 64μ.	24μ.x24μ.
Internal parasite, larva	750μ.	48μ.x 42μ.	24μ.x24μ.
		40μ.x 40μ.	24μ.x24μ.
Nematus pomum larva		56μ.x 40μ.	24μ.x24μ.
		40μ.x 44μ.	24μ.x24μ.
Trypeta solidaginis larva		72μ.x 80μ.	32μ.x32μ.
		60μ.x 62μ.	32μ.x32μ.

In Table III, the measurements given are constant in a large number of individuals for each species, and from the study of these it will be seen:

1. In Dryophanta erinacei the oenocytes reach their maximum size when the larva measures 2½mm. Fig. 93, Pl. XI shows such an oenocyte.

2. No oenocyte shows a threefold increase during the larval development. The average of the largest oenocytes was 64μ.x40μ., nucleus 32μ. while the smallest was 40μ.x40μ. nucleus 24μ.

3.   The oenocytes of the second larval stage are as large as those of the fourth stage.

4.   Among the inhabitants of the gall the largest oenocytes, (Figs. 83 and 84, Pl. X). were found in a Chalcid pupa, of the genus Eurytoma, while in a larva 1½mm. long of the same genus the oenocytes were larger than those of a similar sized larva of Dryophanta erinacei.   Figs. 85 and 86, Pl. X, show such an oenocyte.   It is important to note that these occur in a parasite, which, as pointed out earlier in this paper, does not produce a gall.

5.   A 1¾mm. larva of Synergus erinacei possesses oenocytes, (Fig. 87, Pl. X), larger than those of a similar sized larva of Dryophanta erinacei, yet Synergus erinacei is only an inquiline.

6.   In an internal parasite of Dryophanta erinacei measuring 750μ. the oenocytes are as large as those of a similar sized host.   The parasite does not emerge from Dryophanta erinacei until after the gall has attained full growth, and hence has no part in the production of the gall.

7.   The Tenthredinid, Nematus pomum, which develops in a gall not produced by any product poured forth by the Malpighian vessels possesses oenocytes of considerable size, while the Malpighian vessels are normal, (Figs. 80 and 81, Pl. X).

8.   The same is true of Trypeta solidaginis, an oenocyte of which is shown in Fig. 82, Pl. X.

Now since the largest oenocytes are not found in Dryophanta erinacei, but in a Chalcid parasite which is not a gall-maker, since there in no triple increase in the oenocytes of Dryophanta erinacei, and further, since there is a distinct limit within the range of which the varying oenocytes of all species really fall, it is clear that the conclusion of Rössig is not substantiated by the present investigation.

"The general opinion that they are excretory organs destined to store up urates, especially, as shown by Verson in Bombyx, during the time when the Malpighian vessels do not carry out their function, during molting and pupation."

In general, students of oenocytes have considered them secreting organs, but as Perez has pointed out in "Contributions à l' Étude de Metamorphosis" we do not know what their secretion is.

It is true that Verson considered the cells secretors of urates in Bombyx, and Koschevnikov discusses the urate-laden

oenocytes of the honey-bee, speaking of them as permanent reservoirs which could not free themselves of their products, and had ceased activity. Berlese also describes oenocytes containing urates in many of the species he has studied. Perez, however, has pointed out that these workers have confounded urate cells with oenocytes, and it is significant to note that Berlese in his recent work "Gli Insetti" does not speak of oenocytes bearing urates, but limits that function to urate cells.

The urate-bearing oenocytes that Rössig describes in Andricus Malpighi have the distinct marks of urate cells, and are probably such. Further, he has shown that the injection of chemically pure urates into the plant tissue gives negative results, and therefore urates are not considered factors in gall production. Suppose that we concede to the oenocytes the function of secreting urates, have we gained anything?

According to the above quotation, the urate-secreting function of the oenocytes is performed particularly during the molting and pupating periods when the Malpighian vessels are not functional. It has been shown that the oenocytes do not secrete urates. In all the species we have studied, urate crystals or urate globules have never appeared in the oenocytes. In Dryophanta erinacei we have never observed any unusual activity in these cells during the periods when the Malpighian vessels are not active, and the same can be stated of Holcaspis globulus, Dryophanta polita, Synergus erinacei, and the Eurytoma larva. Moreoever we do not know the chemical constitution of the secretion seen in the vacuoles of the oenocytes. Therefore we have no reason for assigning to the oenocytes the function of secreting urates.

A Possible Correlation in the Development of the Malpighian Vessels and the Oenocytes.

In discussing this phase of the problem, Rössig states that he cannot speak with certainty, but thinks that at least in Dryophanta divisa a correlation exists between the development of the Malpighian vessels and the oenocytes. He presents the following tabulation:

		MALPIGHIAN VESSELS		OENOCYTES	
	LENGTH	CELLS	NUCLEUS	CELLS	NUCLEUS
D. divisa	460μ.	50μ.	36μ.	50μ.	25μ.
" "	600μ.	73μ.	50μ.	100μ.	50μ.
" "	714μ.	115μ.	56μ.	150μ.	59μ.

From this he concludes that the cells of the Malpighian vessels are doubled in size while those of the oenocytes increase threefold.

Now in comparing Table II and Table III, it will be seen that in Dryophanta erinacei there is no indication of any correlation existing between the oenocytes and the Malpighian vessels. The oenocytes have reached their maximum when the larva is in the prepupal stage, and the Malpighian vessels are largest when the larva measures 1¾mm.—approximately the middle of August. As far as our investigation has gone we have found nothing to support the idea of any correlation in the development of the oenocytes and the Malpighian vessels.

CONCLUSION.

The conclusions drawn from the foregoing study of Dryophanta erinacei are as follows:

1.   From a study of the life-history of Dryophanta erinacei we have another illustration of dimorphism in the Cynipidæ.

A.   The agamic form of Dryophanta erinacei produces the oak hedgehog gall on the veins of the white oak leaves, passes through five larval stages extending over a period from the last of June to the first of September. Pupation occurs on the first week in September, and the adults emerge about the fifth of November.

B.   The adults oviposit on the leaf and flower buds of the same tree.

C.   The following spring the eggs hatch, and the larvae produce galls on the leaf scale or the terminal growing points of the buds, from which within two weeks the sexual form of Dryophanta erinacei emerges.

D.   These oviposit on the midrib and lateral veins of the young leaves of the white oak. From the eggs deposited emerge the young larvæ which produce the summer gall.

E.   The sexual form belongs to the genus Dryophanta, and will therefore be known as the sexual form of Dryophanta erinacei, of which the insect, formerly known as Acraspis erinacei is the agamic form.

2.   The study of the parasitic and guest life shows that the following insects inhabit the gall: Decatoma flava (Ashmead); Decatoma querci-lana-dorsalis (Fitch); Decatoma varians

(Walsh); Eurytoma studiosa (Say); Eurytoma auriceps (Walsh) Ormyrus ventricosus (Ashmead); Syntomaspis sp.; Tetrastichus sp.; Synergus erinacei (Bass.)

A. The Chalcids are primarily parasitic on Dryophanta erinacei, and secondarily on each other.

B. The inquiline, Synergus erinacei, is parasitic on the entire life of the gall, mining from cavity to cavity and devouring the larvæ they contain.

C. Eurytoma studiosa and Eurytoma auriceps, and Synergus erinacei have two broods. The spring brood appearing June tenth to fourteenth, and the summer brood appearing from July twenty-fourth to August first.

D. The percentage of parasites, not including the internal parasites, is at least sixty per cent.

3. The Malpighian vessels of Dryophanta erinacei secrete a fluid which stimulates the plant to produce the gall. This is shown by the following:

A. The character of the Malpighian vessels of the sexual and agamic forms of Dryophanta erinacei—their size, cellular structure, and exceptional glandular activity.

B. The character and effect of the secretion poured forth by the Malpighian vessels during gall formation.

C. The ultimate decline and ceasing of marked activity of the tubules when the gall has matured.

D. The increase in the size of the cells of the Malpighian vessels coincident with the development of the gall, and their decrease in size when the demand upon them is withdrawn.

E. A comparison of the Malpighian vessels of Dryophanta erinacei with those of the parasites and the inquilines found in the gall, and particularly the lack of any abnormal secreting activity in the latter.

F. A study of the Malpighian vessels of Holcaspis globulus, and Dryophanta polita, both of which correspond in their action, development, and degeneration to those of Dryophanta erinacei.

G. A comparative study of the Malpighian vessels of Dryophanta erinacei with those of Nematus pomum, Trypeta solidaginis, and Cecidomyia strobiloides shows that all the latter, though gall producers, possess tubules of normal type, which do not pour forth an abundant secretion during gall development, nor when in contact with foreign substances.

H. The study of the Malpighian vessels of species of Braconids and Ichneumons, shows tubules with cells not larger than those of the Chalcids and inquilines. The mode of degeneration however, appears similar to that found in Dryophanta erinacei.

4. The theory of the relation of the oenocytes to gall production as urged by Rössig is not confirmed by this study.

A. His argument is without support from the data furnished by Dryophanta erinacei, Dryophanta polita, and Holocraspis globulus. The oenocytes of the Eurytoma pupa and the larva, Synergus erinacei, are relatively larger than those found in a larva of similar size of Dryophanta erinacei, while the oenocytes of Nematus pomum and Trypeta solidaginis were equal to those found in Dryophanta erinacei.

B. The oenocytes do not secrete urates. Perez has shown this to be true in the ants, and Berlese appears to have now accepted this view. In the oenocytes of the various species studied, we have found no urate crystals or globules.

C. Since we do not know the chemical character of the secretion in the oenocytes, and since there appears to be no unusual activity in these cells during the molting and pupating periods of these species under consideration, we are not convinced that they take the place of the Malpighian tubules during these periods.

Until we know the chemical character of the secretion produced by the oenocytes, we shall only deal in speculation as to the rôle of these cells in insect life.

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EXPLANATION OF PLATES.

PLATE I.

Fig. 1. Oak Hedgehog Gall attached to the midrib of a White Oak leaf.
Fig. 2. Longitudinal section through a Gall. A. Central cavities; B. Lateral Cavities.
Fig. 3. Agamic form of D. erinacei ovipositing on the bud of White Oak.
Fig. 4. Female, sexual form of D. erinacei.
Fig. 5. Pupa of agamic form of D. erinacei.

PLATE II.

Fig. 6. Bud scale with eggs of agamic form attached.
Fig. 7. Bud scale with enlarged gall, egg-shell still attached.
Fig. 8. Longitudinal section through Oak Hedgehog Gall showing Peripheral Cavity.
Fig. 9. Bud scale on which young gall is forming with empty egg-shell attached.
Fig. 10. Terminal Galls.
Fig. 11. Oblique section through Oak Hedgehog Gall showing where S. erinacei has mined from A – B.
Fig. 12. Longitudinal section through Oak Hedgehog Gall showing where S. erinacei has mined from A – B, and is breaking down the wall at C.

PLATE III.

Fig. 13. Mandible of Agamic form of D. erinacei.
Fig. 14. Maxilla of Agamic form of D. erinacei. A. Cardo; B. Stipes; C. Palpus; D. Galea.
Fig. 15. Labium of Agamic form of D. erinacei. A. Palpus; B. Glossa; C. Paraglossa.
Fig. 16. Antenna of Agamic form of D. erinacei.
Fig. 17. Two distal segments of antenna showing sensory pits.
Fig. 18. Aborted wings of agamic form of D. erinacei.
Fig. 19. Larva of agamic form of D. erinacei.
Fig. 20. Egg of agamic form of D. erinacei.
Fig. 21. Mandible of sexual form of D. erinacei.
Fig. 22. Maxilla of sexual form of D. erinacei. A. Cardo; B. Stipes; C. Palpus; D. Galea.
Fig. 23. Labium of sexual form of D. erinacei. A. Palpus; B. Glossa; C. Paraglossa.
Fig. 24. Wings of sexual form of D. erinacei.
Fig. 25. Egg of sexual form of D. erinacei.
Fig. 26. Scutellum of sexual form of D. erinacei.
Fig. 27. Larva of sexual form of D. erinacei.
Fig. 28. Antenna of sexual form of D. erinacei.
Fig. 29. Distal segments of antenna showing sensory pits.

PLATE IV.

Fig. 30. Larva of internal parasite from agamic form of D. erinacei.
Fig. 31. Egg of Ormyrus ventricosus.
Fig. 32. Egg of Decatoma flava containing embryo.
Fig. 33. Mandible of Eurytoma larva.
Fig. 34. Larva of Decatoma flava.
Fig. 35. Larva of Eurytoma sp.
Fig. 36. Diagram showing location of setæ on segments of larva of S. erinacei (spring brood).
Fig. 37. Eurytoma egg with larva emerging.
Fig. 38. Larva of S. erinacei (summer brood).
Fig. 39. Egg of S. erinacei (summer brood).
Fig. 40. Larva of S. erinacei (spring brood).
Fig. 41. Egg of S. erinacei (spring brood).

PLATE V.

Fig. 42.   Diagram showing location of setæ on segments of larva of Decatoma
flava.
Fig. 43.   Diagram showing location of setæ on segments of Eurytoma larva.
Fig. 44.   Diagram showing location of setæ on segments of larva of S. erinacei
(summer brood).

PLATE VI.

Fig. 45.   Longitudinal section through larva of agamic form D. erinacei showing
Larval Malpighian tubule, Valve, mid-intestine hind-intestine.
Fig. 46.   Longitudinal section through larva of agamic from of D. erinacei showing
larval Malpighian vessel, mid-intestine, hind-intestine, and hypo-
dermis.
Fig. 47.   Longitudinal section showing larval Malpighian vessel extending the
length of the mid-intestine.
Fig. 48.   Larval Malpighian tubules as dissected out from D. erinacei, agamic
form.
Fig. 49.   Degenerating larval Malpighian tubules, and adult vessels forming, as
dissected out from D. erinacei, agamic form.

PLATE VII.

Fig. 50.   Cross section from D. erinacei, agamic form, showing cell of larval
Malpighian tubule in the lumen of the intestine, and adult vessel
forming.
Fig. 51.   Longitudinal section from larva of D. erinacei, agamic form, showing
cell just breaking away into the lumen of the intestine.
Fig. 52.   Larval Malpighian tubules of D. erinacei greatly reduced, and adult
vessels nearing maturity.
Fig. 53.   Larval Malpighian tubules of D. erinacei reduced to a few cells, adult
vessels well developed.
Fig. 54.   Longitudinal section of degenerating larval Malpighian vessel, with
adult tubules forming from H. globulus, agamic form.
Fig. 55.   A portion from a longitudinal section of a larva of D. polita, agamic
form. showing degenerating larval tubules, and adult vessels forming.
Fig. 56.   Longitudinal section through cells of degenerating larval Malpighian
vessels of H. globulus.

PLATE VIII.

Fig. 57.   Larval and adult Malpighian vessels of H. globulus as dissected out.
Fig. 58.   Portion of longitudinal section of larval Malpighian vessel of H. globulus.
Fig. 59.   Longitudinal section through degenerating cells of Malpighian vessel
of H. globulus.
Fig. 60.   Larval Malpighian vessels of S. ernacei as dissected out.
Fig. 61.   Longitudinal section through cells of larval Malpighian vessel of S.
erinacei.
Fig. 62.   Larval Malpighian vessels of Eurytoma larva as dissected out.
Fig. 63.   Longitudinal section through cells of Malpighian vessel of a Eurytoma
larva.

PLATE IX.

Fig. 64.   Larval Malpighian vessel of D. flava as dissected out.
Fig. 65.   Longitudinal section through cells of Malpighian vessel from Nematus
pomum.
Fig. 66.   Longitudinal section showing attachment of larval Malpighian tubules
to alimentary tract of N. pomum.
Fig. 67.   Section showing larval Malpighian vessels, and adult tubule just
appearing.
Fig. 68.   Longitudinal section through a portion of a larval Malpighian tubule
of T. solidaginis.
Fig. 69.   Longitudinal section through a portion of a larval Malpighian tubule
of C. strobiloides.

Fig. 70. Longitudinal section through a portion of a larval Malpighian tubule
of D. erinacei, sexual form.
Fig. 71. Longitudinal section through a portion of a larval Malpighian vessel
of an Ichneumon.
Fig. 72. A cross section of a larval Malpighian tubule of D. erinacei, agamic form.

PLATE X.

Fig. 73. A cross section of a larval Malpighian vessel of the same species showing
degenerating cells.
Fig. 74. Cross section of an adult Malpighian tubule of D. erinacei.
Fig. 75. Cross section of larval Malpighian tubule of N. pomum.
Fig. 76. Cross section of larval Malpighian tubule of T. solidaginis showing
phagocytes.
Fig. 77. Cross section of a larval Malpighian vessel of C. strobiloides.
Fig. 78 and 79. Oenocytes from larva of N. pomum.
Fig. 80 and 81. Oenocytes from larva of internal parasite in D. erinacei.
Fig. 82. Oenocyte from larva of T. solidaginis showing vacuoles.
Fig. 83. Oenocyte from thorax of Eurytoma pupa.
Fig. 84. Oenocyte from the abdomen of a Eurytoma pupa.
Fig. 85. Oenocyte from the thorax of a Eurytoma larva $1\frac{3}{4}$mm.
Fig. 86. Oenocyte from the abdomen of a Eurytoma larva $1\frac{3}{4}$mm.
Fig. 87. Oenocyte from S. erinacei containing vacuoles.

PLATE XI.

Fig. 88. Oenocytes from the abdomen of a larva of D. erinacei $1\frac{1}{2}$mm.
Fig. 89. Oenocytes from the abdomen of a larval of D. erinacei $2\frac{1}{4}$mm.
Fig. 90. Oenocytes from the abdomen of a larva of S. erinacei.
Fig. 91. Oenocytes from the thorax of a larva of H. globulus.
Fig. 92. Oenocytes from the abdomen of a larva of H. globulus.
Fig. 93. Oenocyte from the thorax of a larva of D. erinacei $2\frac{1}{2}$ mm.
Fig. 94. Oenocyte from the abdomen of a larva of D. erinacei $2\frac{1}{2}$mm.
Fig. 95 and 96. Oenocyte from a larva of D. erinacei 2mm.
Fig. 97. Oenocyte from a larva of D. erinacei $1\frac{1}{4}$mm.
Fig. 98. Oenocyte from a larva of D. erinacei 1mm.

ABBREVIATIONS.

c. l. m. t. ....Cell of larval Malpighian tubule
e. .... Egg
h. int. .... hind-intestine
hyp. .... hypodermis
i. m. t. ....Imaginal Malpighian tubule
md. .... Mandibles
mx. .... maxilla
m. d. .... mid-dorsal
m. v. .... mid-ventral
m. int. ....mid-intestine
la. ....labium
l. ....lateral
l. ....lumen
l. m. t. ....Larval Malpighian tubules
oe. ....oenocytes
ph. .... phagocytes
s. g. ....scale galls
s. p. ....sensory pits
s. .... setæ
t. g. ....terminal galls
vac. ....vacuoles